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A PHOTOGRAPHIC SURVEY OF BENTHIC FISHES  
IN THE RED SEA AND GULF OF ADEN, WITH  
OBSERVATIONS ON THEIR POPULATION DENSITY,  
DIVERSITY, AND HABITS

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WITH FOUR PLATES

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No. 2 — *A Photographic Survey of Benthic Fishes in the Red Sea and Gulf of Aden, with Observations on their Population Density, Diversity and Habits*<sup>1</sup>

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### INTRODUCTION

Automatic photography of the deep-sea floor began in 1940 (Ewing, Vine and Worzel, 1946). Since that successful beginning, many thousands of bottom photographs have been taken, but relatively few have been used by marine biologists. Concerning deep-sea fishes, interesting observations and photographs have been made from bathyscaphes (see, for instance, Fages et al., 1958). But more can be learned by analyzing a good series of pictures taken with an automatic camera (see Laughton, 1963). By taking a census of the fishes revealed, and knowing the area surveyed by the camera, an estimate can be obtained of their population density. At the same time, the sizes of these fishes should be known, so that due regard can be given to their weight. In this way, a measure can be got of the fish biomass supported per unit area of the deep-sea floor at different places and depths. One aim of this paper is to introduce such research. Further such analysis of photographs taken in parts of the North Atlantic is in progress.

The present study is based on some 2260 photographs, which were taken under the direction of Dr. J. W. Graham during ATLANTIS Cruise 242, June 1958. Six photographic stations were made, four in the Red Sea and two in the Gulf of Aden (see Table 1, and Figure 1). Though the fishes photographed often are not identifiable to family or smaller groups, it is possible to get a fair idea of the number of species involved. In the present instance, the photographs corroborate and extend earlier evidence that the Gulf of Aden contains more kinds of

<sup>1</sup> Woods Hole Oceanographic Institution Contribution No. 1402.

deep-sea fishes than exist in the Red Sea.<sup>1</sup> After considering this aspect, we give a brief, comparative review of the diversity of deep-sea fishes in certain basins.

Scrutiny of the clearest photographs can also reveal much of the habits and habitats of deep-sea fishes. Some, for instance, rest on the bottom; others swim over the bottom. Our concern here is with benthopelagic forms that have a well developed swimbladder, notably with species of halosaurs, morids and macrourids. In particular, we consider the hovering and swimming postures of halosaurs and macrourids with relation to the expected dynamics of their fin pattern. Again, further work on such aspects is in progress.

We are grateful to Dr. J. B. Hersey both for making the photographs available to us, and for his comments on the manuscript.

Dr. R. H. Backus gave us many valuable criticisms and suggestions.

Details of the cameras used on ATLANTIS Cruise 242 were supplied by Dr. H. E. Edgerton.

Gloria Gallagher, the present curator of the photograph collection, has been most helpful; her predecessor in that office, Jane F. Broughton, prepared the data from which areas were computed.

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## TECHNICAL ASPECTS

A pair of Edgerton cameras was used, rigged to provide stereo pictures at 15-second intervals. The cameras are shutterless, and were fitted with 50 mm focal length (in water) lenses; 100 watt/second electronic flash made the exposures and the ship's rate of drift determined the spacing between shots.

The rough bottom topography at these stations, together with the ship's motion, made it impossible to keep the cameras a uniform distance off the bottom, but the cameras' position, monitored with the aid of 12 ke sonar (the transducer mounted on

<sup>1</sup>A list of the deep-sea fishes recorded from the Gulf of Aden appears at the end of this paper.

the camera frame), was kept between 1.5 and 3.5 meters off bottom for about two-thirds of the frames; the focus was set for 2 meters. Bottom areas covered in most of the pictures, then, are from 0.8 to 4.2 square meters, but the areas used in computing densities are totals of separate determinations for each picture, using camera-to-bottom distances from the ship's depth recorder.

Identifications from top views are not easy: for one thing, the dorsal aspect of a fish is not often figured in the literature, and for another, diagnostic features are likely to be obscured. Stereo photographs are a great help and, fortunately, most of the stereo pairs from these stations were successful (about one-quarter of the pictures are single-frame only). Features, such as filamentous rays, quite invisible in one of a stereo pair may be obvious when both are viewed together. Shadows, too, show structures otherwise concealed, pelvic fins for example.

The possible effect of the apparatus on the animals, particularly the flash and motor noises, is often questioned, but these pictures and many others give little evidence that bottom fishes are much disturbed by it. The small puffs of sediment raised by a fish darting off the bottom are seen rarely; furthermore, where the drift is slow, the same individual often appears in a series of pictures. For instance, one eel kept its position, a foot or so off the bottom, in 9 successive frames.

## POPULATION DENSITY

With increasing depth, larger animals of the deep benthos become less numerous and less diverse. If values of these two faunal features are plotted against the depth, the graph described for the larger benthic invertebrates is exponential in form (Zenkevitch, 1963). The same relationship holds for benthic fishes. Their density and diversity are greatest over the upper reaches of the continental slope. At levels from 1000 to 2000 meters, there is a steady fall in the numbers of individuals and species, but beyond 2000 meters the gradient of fall is more pronounced. Somewhere between depths of 2000 and 3000 meters comes a transition to a restricted fauna of abyssal fishes.

Preliminary analysis of the number of fishes seen in bottom photographs taken at depths from 360 to 1960 fathoms (658 to 3584 meters) in parts of the North Atlantic shows very well the exponential nature of the decline. Some such decline in density and diversity must also occur in the Red Sea and Gulf of Aden.

For the latter area, these may be seen from Norman's (1939) report on the fishes of the John Murray Expedition. While the catches show that the density and diversity of benthic fishes are greatest from 200 to 500 meters, there is no abrupt change in these quantities from 500 to 1500 meters. In the present context, the camera lowerings at Station 1 (680 fathoms, 1240 meters) are thus above a depth where marked changes in density and diversity lead, so to speak, to the poor abyssal fauna. It is also fortunate that two stations in the Red Sea (3 and 6) are at much the same depth. Relevant comparisons can be made

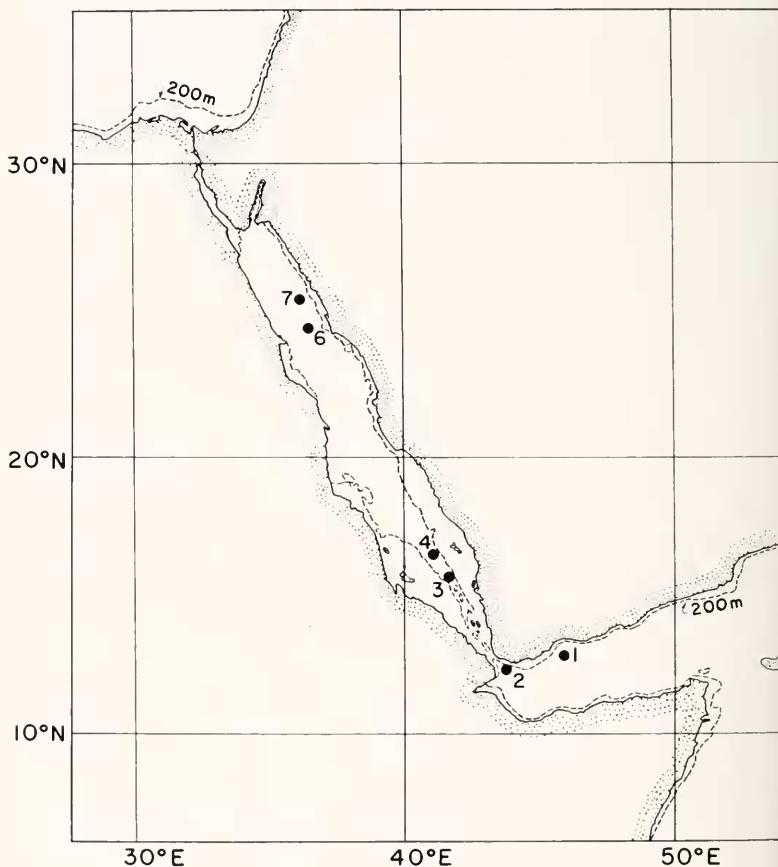


FIG. 1. Photographic stations in the Red Sea and Gulf of Aden.

TABLE 1

	Station	Position	Depth Fathoms (Meters)	Area Surveyed (Square Meters)	Number Specimens	Density (Fish/M <sup>2</sup> )	Number Species
Gulf of Aden	2	12°19.5'N, 43°42.4'E	165 (300)	1750	19	1/90	15-16
"	1	12°51.0'N, 45°57.5'E	680 (1240)	1045	42	1/25	19
Red Sea	3	15°42.5'N, 41°43.0'E	660 (1210)	ca. 400	0	0	0
"	6	24°29'N, 36°27.5'E	610 (1115)	1660	19-23 <sup>1</sup>	1/87-1/70	4
"	4	16°34'N, 41°04'E	1000 (1830)	ca. 300	3	1/100	1
"	7	25°21.7'N, 36°06.5'E	1200 (2195)	850	7-10 <sup>1</sup>	1/120-1/85	1

<sup>1</sup> The same specimen may appear in more than 1 frame; thus, the range in numbers.

between these two stations and the one in the Gulf of Aden. The two deeper Red Sea stations (4 and 7) must be taken on their own, as should the shallow station (2) at the entrance to the Gulf of Aden (see map and Table 1).

The area surveyed by the camera at each station may be seen in Table 1. Even disregarding station 3, where no fishes were photographed, the area sampled at the 600-700 fathom depth was greater in the Red Sea than in the Gulf of Aden.

Data in Table 1 show that the population density at the 680 fathom (1240 meters) Gulf of Aden station (1 fish/25 m<sup>2</sup>) is about three times the estimate for the 610 fathom (1115 meters) station in the Red Sea (1 fish/87 m<sup>2</sup>). But, except for three photographs, all of the pictures at the latter station represented one small species of shark (length about 2 feet or 0.6 meter). The mean length of fishes in the Gulf of Aden was about 1 foot (0.3 meter). The mean weight of individual fish in the Red Sea, then, may well have been about six times that in the Gulf of Aden.<sup>1</sup> Perhaps the difference in density between the two areas is more than counterbalanced by the size factor, but it would seem fair to conclude that both areas support a roughly equivalent fish biomass.

In this respect it is worth recording that measurements made from ATLANTIS (Cruise 242) over the period May 16 to June 28, 1958, show that levels of primary production in the Red Sea and Gulf of Aden were low and of much the same quantity in the two places (Yentsch and Wood, 1961). The authors compare these values to those in poorly productive areas such as the Sargasso Sea. On an annual basis, though, parts of the Gulf of Aden, where upwelling occurs, may be more productive than the Red Sea. But whether this is true of that part of the Gulf in the neighborhood of station 1 (see Fig. 1) can hardly be predicted.

Densities are somewhat lower (*ca.* 1 fish/100 m<sup>2</sup>) at the deep stations 4 and 7 (1000 and 1200 fathoms, or 1830 and 2195 meters) in the Red Sea. In terms of biomass, comparison is most readily made between stations 7 and 6; for at the former all the fish taken represented the small species of shark that appeared in most of the pictures from station 6. There is no more than a slight fall in biomass in descending from 610 to 1200 fathoms (1115 to 2195 meters). Between these levels in the

<sup>1</sup> In fishes of comparable form, the weight increases about six-fold for a two-fold increase in length.

North Atlantic there is a gradual (and rather gentle) decline in the population densities of fishes.

At the shallow Gulf of Aden station 2 (165 fathoms, or 302 meters), the density (1 fish/90 m<sup>2</sup>) is surprisingly low. Is this a biological reflection of the hydrographical conditions in this region? Station 2 is on the slope of the Red Sea sill. During part of the summer, at least, warm and highly saline water (20° C and 38 ‰) spills out of the Red Sea and flows down the sill (Neumann and McGill, 1962). In winter, according to Thompson (1939), this outflow is much greater. The hydrographic regime would thus seem to be both unusual and variable.

### DIVERSITY

Though the photographs rarely capture enough detail of a fish for specific identification, prolonged scrutiny has convinced us that the camera photographed 4 different species in the Red Sea and 19 at station 1 in the Gulf of Aden. Since the total area surveyed at 600-700 fathoms in the first region (3100 m<sup>2</sup>) is three times that covered in the second (1045 m<sup>2</sup>), it looks as though fish diversity in the Gulf of Aden is at least 5 times that in the Red Sea (Table 1).

Before considering this faunal difference, we give here an account of the forms involved. As already mentioned, at station 7 in the Red Sea the records were confined to one species of shark. All but three of the individuals photographed at station 6 were of this same species. This shark has two (spineless)

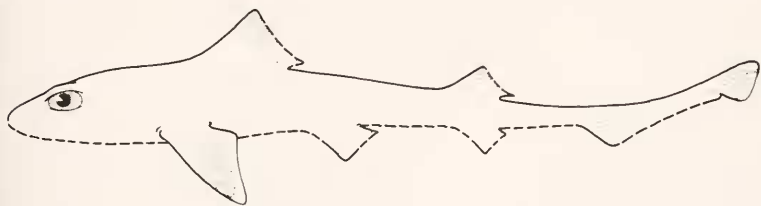


FIG. 2. Reconstruction of a Red Sea shark (from several pictures showing dorsal views).

dorsal fins and an anal fin. It is thus a galeoid (Fig. 2, and Pl. 1). But despite an extensive search of the literature, we are unable to assign this shark to any known family of galeoids. Dr. J. A. F. Garrick, who kindly looked at the photographs,

thought the fish might either belong to the Triakidae (=Musalidae) or Carcharhinidae. Yet the shape and fin pattern of this shark, particularly the forward position of the first dorsal, are unlike those of any triakid or carcharhinid genus. Perhaps we have a new genus of sharks.

The three other species from station 6 are teleosts; one of these is some kind of eel.

At station 1 in the Gulf of Aden, the commonest fish, shown in nine frames, is a morid with a pair of long rays in each pelvic fin. These rays (Fig. 3) are proportionately longer than those in *Physiculus roseus* Alcock, the only known morid from the Gulf (see check list). Though *P. longifilis* Weber has two long pelvic rays, perhaps *Laemonomodes* Gilchrist is closest to our fish. Halosaurs, probably belonging to one species, were taken in four frames (Pl. 2), and macrourids, representing at least three

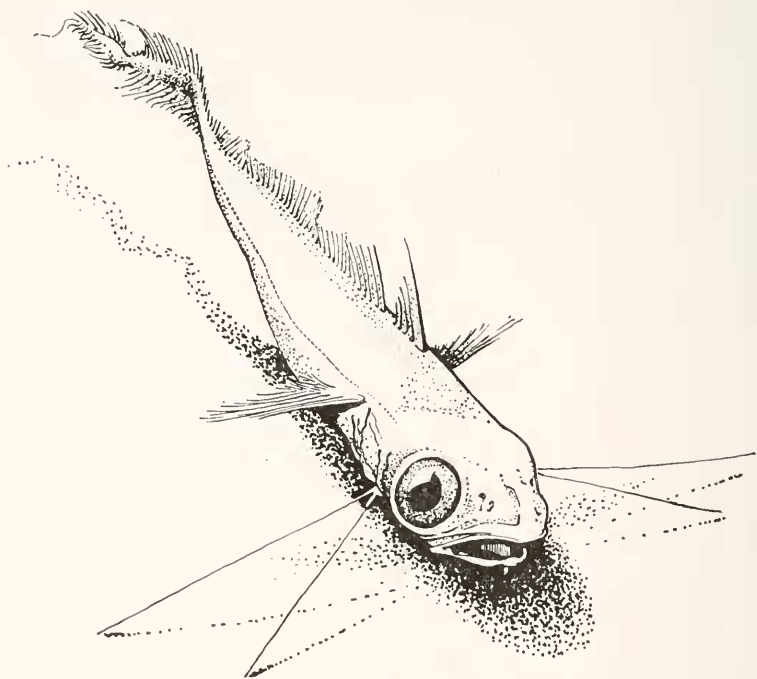


FIG. 3. Reconstruction of a morid fish having two long, moveable rays in each pelvic fin. This was the commonest fish photographed in the Gulf of Aden.

species, in another five frames. One of the best pictures (Pl. 2) is of a bathygadine macrourid with a long filamentous ray in the first dorsal and each paired fin. A second species is a *Coelorhynchus*. A fish very like a *Bathysaurus* and a rhinochimaerid, probably *Harriotta* (Pl. 3), are each seen in one frame. Of the remaining species, two are eels and one may be a lizard-fish (Synodontidae). The others are not identifiable to groups.

At station 2 in the Gulf of Aden photographs of 15 or 16 species were taken. There is a dogfish (*Halaelurus*, close to *quagga* Alcock, Pl. 4), a *Rhinobatus*, a rajid, a synodontid (Pl. 4), a peristediid and a cynoglossid. The remaining fishes, while recognizable as distinct species, cannot be assigned to families. The community is clearly unlike that revealed by the camera at the deeper Gulf of Aden station.

Returning to the contrast in diversity between the benthic fishes of the Red Sea and Gulf of Aden at depths of 600 fathoms and beyond, our findings corroborate and extend those of deep-sea expeditions. In the check list of deep-sea fishes from the Gulf of Aden (Table 2), there are 55 benthic species. Knowledge of the corresponding fauna in the Red Sea comes entirely from the 'Pola' Expedition (1895), which dredged at about 60 stations between depths of 200 and 2000 meters. While a dredge is not the best gear for catching fishes, five species were taken (Fuchs, 1901): *Hoplostethus mediterraneus* Cuvier and Valenciennes, a pleuronectid, a leptocephalus, *Chauliodus sloani* Schneider, and *Bregmaceros maclellandi* Thompson. The first two are to be regarded as benthic in habit. These two, together with the four seen in the photographs, are the only benthic deep-sea fishes known from the Red Sea.

The fauna of bathypelagic fishes is also poorer in the Red Sea than in the Gulf of Aden. In the Gulf, 32 species are given in the check list. There are nine Red Sea species: *Maurolicus mucronatus* Klunzinger, *Vinciguerria* sp., *Stomias affinis* Günther, *Astronesthes martensii* Klunzinger, *Chauliodus sloani* Schneider, *Diaphus coeruleus* (Klunzinger), *Benthosema pterota* (Alcock), *Bregmaceros maclellandi* Thompson, and a paralepidid (see also Marshall, 1963).

The evolution of a diverse fauna requires time and a favorable environment. The latter, which must obviously be accessible, needs to be stable, though a relatively high and constant temperature, both through the year and geological time, is not everywhere an essential condition for great diversity. Prolonged

exploration at fixed points in the tropical and subtropical ocean has revealed that the deep-sea fish fauna is remarkably diverse there (Marshall, 1963). Such species live in waters that are cool or cold, and that have evidently been so for a great time. Indeed oxygen-isotope measurements on calcareous benthic foraminiferans from deep-sea cores indicate that the temperature of the bottom water in the eastern equatorial Pacific has decreased from about 10° C in mid-Oligocene times to about 2° C in the late Pliocene (Emiliani and Flint, 1963). But constant water temperatures alone are not enough to permit a high diversity, otherwise we might expect such to have evolved in polar waters. As is well known, the number of species of deep-sea fishes in polar (and temperate) waters is relatively low. But in these waters phytoplankton production is restricted to a few months in the year. In subtropical and tropical waters the growing season is more or less continuous, which indicates that a fairly steady supply of food through the year is linked somehow to faunal diversity. The reasons for this are not immediately obvious, and, so far as deep-sea fishes are concerned, will remain obscure until detailed studies are made of their food.

Considering these factors, why are there so few kinds of deep-sea fishes in the Red Sea? Regarding the invertebrates (mainly shallow water species) and their high degree of endemism, Ekman (1953) wrote that "... we know with considerable accuracy the amount of time which has been available for the formation of new species in the Red Sea. This sea came into existence at the end of the Pliocene or the beginning of the Quaternary period (Pleistocene) when the large inland sea which formerly covered the "erythraic" depression first joined up with the Mediterranean and later on with the Indian Ocean. The transition from Pliocene to the Quaternary period occurred roughly one million years ago, and this time was accordingly sufficient for a fairly large number of animal species to undergo changes of a magnitude which differentiated them as new species."

Time has also been sufficient for the evolution of a fairly high degree of endemism (*ca.* 10 per cent) in a diverse fauna of reef fishes in the Red Sea. These came from the Indian Ocean, either as adults or young stages. They were not barred by the sill, nor by the hydrographical conditions that depend on the sill. The same is true for a few species of deep-sea fishes. If certain species have managed to enter, why not more?

Concerning the bathypelagic species, Marshall (1963) concluded that physical conditions in the Red Sea, particularly the

warm isothermal structure, are so unlike those in the open ocean that invaders would have to be very adaptable to gain a footing. Such genetic plasticity is likely to be rare. For the benthic deep-sea fishes, the sill, which rises to within 150 meters of the surface, would be a barrier except to markedly eurybathic species. Moreover, few benthic species appear to pass their early life history in the surface waters, so reducing their chances of being carried into the Red Sea. In any event, the high temperatures of the bottom water (*ca.* 21.5° C) must be a barrier to all but the species that live in the relatively warm waters over the upper part of the continental slope. As Balss (1931) found, certain benthic decapods that live in the deeps of the Red Sea are found at shallower levels in the outer oceans. But cosmopolitan deep-sea decapods, which live below a depth of 1500 meters, seem to be absent from the Red Sea.

The Red Sea holds a poor fauna of deep-sea fishes. Is the same true of other deep basins having shallow sills, but where there is little or no stagnation in the water column? What of the Sea of Japan, the Mediterranean, the Gulf of Mexico and the Sulu Sea?

Diversity is least in the first, moderate in the Mediterranean, but quite high in the last two basins. Some 20 species, mostly benthic, are known from the Sea of Japan (Zenkevitch, 1963). There are about 550 species of fish in the Mediterranean, of which 120 live at depths of 200 meters or more (Tortonese, 1959). At least three-quarters of the deep-sea species are bathypelagic. Four of the benthic species are known to live at depths beyond 2000 meters.

Though a check list has yet to be made, it is clear that the Gulf of Mexico contains a rich fauna of deep-sea fishes. Grey (1958 and 1959) has recorded some 50 species of which about a third are bathypelagic. Bigelow and Schroeder's work (e.g. 1962 a, b) shows that the Gulf contains a diverse fauna of batoid fishes at moderate depths. There are also at least 30 species of macrourid fishes (Marshall, 1964). The number of macrourids is also a good guide to diversity in the Sulu Sea. Gilbert and Hubbs (1920) list 40 species, of which 16 are endemic.

The Red Sea and the Sea of Japan thus contain few species of deep-sea fishes. In contrast, the Gulf of Mexico and the Sulu Sea have rich faunas. Some of the factors favoring or restricting diversity have been mentioned earlier (p. 233), but can one assume that the number of species, whether in rich or poor basins, is related to a common set of factors?

Comparison of the Red Sea and the Sea of Japan soon shows that one must be more circumspect. The geological history of the latter is somewhat obscure, though it may, like the Red Sea, have assumed its present form at the end of the Pliocene (Zenkevitch, 1963). It is like the Red Sea in being isolated from the open ocean by a sill that rises close to the surface. But it differs sharply from the Red Sea in being isothermally cold below the level of the sill. In winter, cooled waters sink along the slopes causing temperatures between  $1^{\circ}$  and  $0^{\circ}$  C below a depth of 150 meters. Regarding plankton production, the annual growing season is probably more or less continuous in the Red Sea. In the Sea of Japan there are spring and autumn blooms (Zenkevitch, 1963).

The sill forming the Sea of Japan, like that at the mouth of the Red Sea, will bar most kinds of benthic deep-sea fishes. Once over the sill, an invading animal faces either abnormally cold or hot waters below a level of 150 meters. It is not surprising, then, that the bathypelagic fauna of the Red Sea consists of forms that live at upper, and therefore warm, mid-water levels in the outer ocean. Perhaps this fauna is more diverse than the benthic one. In the Sea of Japan, on the other hand, nearly all species belong to benthic or deep bathypelagic groups; this is understandable considering the cold waters at depths below sill level. One exception, *Maurolicus japonicus*, occurs in the upper reaches of the bathypelagic zone in the outer ocean. In the Sea of Japan it presumably lives near the lower limit of the warm surface layer.

The two basins with a rich fauna of deep-sea fishes may be of much the same geological age as the Red Sea and the Sea of Japan. The Gulf of Mexico seems not to have become a deep-sea basin until late Tertiary times (Lynch, 1954). According to Kuenen (1950) the deep-sea morphology of the Moluccas, which includes the Sulu Sea, is entirely of Upper and post-Tertiary development. But both basins have deeper sills than the Red Sea and the Sea of Japan. The Gulf of Mexico leads to the Atlantic over an 800-meter sill and to the Caribbean over a sill about 1600 meters in depth. The sill dividing the Sulu Sea from the South China Sea is nowhere more than 400 meters below the surface.

While the Gulf of Mexico is isothermal (at about  $4^{\circ}$  C) below a level of 1200 meters, temperatures in the Sulu Sea are close to  $10^{\circ}$  C at depths from 1000 meters to the bottom. The regimes of temperature are thus less stringent than those in the Red Sea

and the Sea of Japan. But the higher bottom temperatures in the Sulu Sea, and, perhaps, the relatively shallow sill, have precluded the invasion of abyssal species, judging by the macrourid fauna. In the Gulf of Mexico there is a fairly diverse fauna of abyssal benthic fishes (Grey, 1958).

Besides having more suitable conditions of temperature than those obtaining in the 'poor' basins, the Sulu Sea and the Gulf of Mexico are close to oceanic areas containing rich faunas of deep-sea fishes. There are thus more potential invaders than exist outside the Sea of Japan. The annual plankton cycle in both the Sulu Sea and the Gulf of Mexico is presumably of the stable tropical type.

Though geologically young, the Gulf of Mexico and the Sulu Sea contain relatively rich deep-sea faunas. Some of this diversity is borrowed, some created *in situ*. Concerning the Sulu Sea, one must conclude that the endemic species have evolved during the last million years or so. The situation in the Gulf is more complicated. Some species have come from the Atlantic, some from the Caribbean, while a third group is presumably the result of local speciation. Thorough exploration of the Gulf and Caribbean will be needed before we can be sure of the endemic species. Regarding the species that are common to both but absent from the Atlantic, there seems no way of deciding where they evolved. Perhaps speciation has been greater in the Caribbean. It is also a basin, and is older than the Gulf of Mexico.

## HABIT AND HABITAT

Underwater photographs are valuable in resolving doubts regarding the living spaces of deep-sea fishes. Trawls catch fish as they are hauled to the surface, and may thus contain pelagic as well as benthic species. For the most part, near-bottom photographs have confirmed suspicions, based largely on the form, fin pattern and position of the mouth, as to which groups are benthic in habit. Certain sharks (e.g. *Etmopterus*), chimaeras, bathypteroids, *Bathysaurus*, halosaurs, macrourids, morids and brotulids have been photographed on, or close to, the bottom.

Fishes of the last four groups, which have a capacious swim-bladder, should be able to hover and swim with ease over the deep-sea floor (Marshall, 1960). Again, near-bottom photographs provide valuable evidence that these groups are benthopelagic

in habit.<sup>1</sup> Furthermore, close study of the pictures reveals the attitudes adopted in hovering or swimming.

The macrourids are of particular interest. Most of the present photographs, and many more taken in parts of the Atlantic Ocean, show that macrourids wander nose-down over the sediments, the long body axis being inclined at a slight angle to the bottom (Fig. 4). Considering the dynamics of their fin

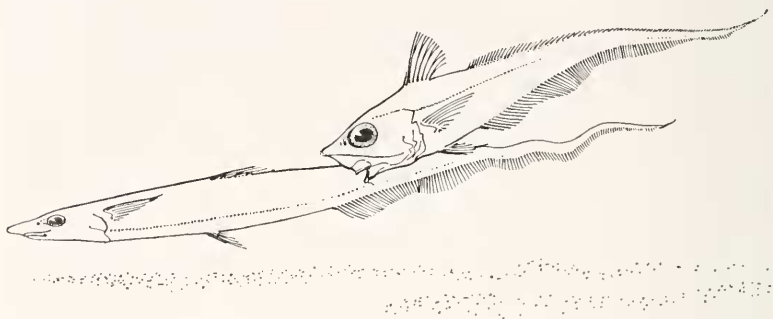


Fig. 4. A halosaur (left) and a macrourid (right), showing the snout-down posture adopted when hovering or swimming. Note the convergence of fin pattern.

pattern, this attitude is to be expected. In most macrourids the rays of the anal fin are considerably longer than those of the second dorsal. As the tail is undulated—and pictures of macrourids often catch the posterior half in sinusoidal motion—the side to side swing of the anal fin will generate a lift, and thus depress the head. The action is rather like that of a heterocercal tail fin. A lift can also be got from undulations of the anal fin itself. When analyzing the motions of the pectoral and dorsal fins of a seahorse, Breder and Edgerton (1942) show that two vectors are involved “. . . in connection with the resultant of the simple wigwagging of fin rays and in the consequent passage of a wave along such a series of identical members.” One component of the resultant thrust is along the axis of the fin; the other is in the same plane but perpendicularly away from the axis. When the long anal fin of a macrourid is set in wavy motion it will thus generate a lift as well as drive the animal forward.

<sup>1</sup> A few species of macrourids are bathypelagic (Marshall, 1964).

The present photographs and others show that halosaurs adopt a slightly inclined posture like that of a macrourid. Again, this is to be expected. Halosaurs also have a long tail and an anal fin with long rays, but the single dorsal member has a short base. Undulations of the tail and anal fin will again drive the animal forward and incline it head-down to the sediments. The photographs often show halosaurs with short wave undulations passing down the posterior half to a third of the tail. But longer wave, eel-like undulations have also been seen.

A head-down attitude is apt in a fish with jaws suspended underneath the snout. All halosaurs and most macrourids have such jaws, which are more easily able to pick food organisms off the bottom. Moreover, the head, which ends in a triangular snout, can be used to root in the oozes, so turning up food organisms. The reinforced snout of a macrourid or a halosaur is thus a decidedly useful structure.

The bathygadine macrourids are unlike the macrourine species not only in having a terminal mouth and long gill rakers but their fins show certain differences as well. The salient feature is that the second dorsal fin has rays that are equal or greater in length than those of the anal fin. If the latter differential holds, one might expect the fish to swim with a slight head-upward inclination to the horizontal. In this respect, it is interesting that the photograph of a bathygadine rat-tail (Pl. 3) which is particularly clear, shows it swimming more or less parallel to the bottom. The posture is plainly different from that shown in a number of other photographs of rat-tails.

Lastly, certain photographs of the morid that is common in the Gulf of Aden show that it swings the long rays of the pelvic fin through an arc of about  $60^\circ$ . By this means the animal (Fig. 3) scans the oozes, presumably with tactile and gustatory endings on the fin rays.

## SUMMARY

During ATLANTIS Cruise 242, May to June, 1958, six photographic stations were made, four in the Red Sea and two in the Gulf of Aden. Over 2000 bottom photographs were taken, many of which show deep-sea fishes.

Analysis of these photographs shows that at depths around 600 meters the density of fishes in the Gulf is about three times that in the Red Sea. But in terms of biomass (the Red Sea pictures being mainly of a two-foot shark) there is not much difference between the two regions.

Though the Red Sea has not been well explored, the photographs support earlier indications that the Gulf of Aden contains a more diverse fauna of benthic, deep-sea fishes. This is also true of the bathypelagic fauna. After considering the factors that seem to favor or restrict diversity in the deep sea, we conclude that the very shallow sill and the unusually warm, isothermal structure of the water below sill level make the Red Sea unsuitable to all but a few very adaptable species of deep-sea fishes.

A faunal comparison of deep-sea basins shows that the Sea of Japan, like the Red Sea, contains relatively few kinds of deep-sea fishes. But the factors restricting diversity are certainly not the same for the two regions. By contrast, the Gulf of Mexico and the Sulu Sea have rich faunas. Some of this diversity is borrowed from the open ocean, some created *in situ*, seemingly during the last million years or so.

Study of the clearest photographs can show much of the habits and habitats of deep-sea fishes. Attention is drawn to benthopelagic species with a well developed swimbladder, notably the halosaurs, macrourids and morids. With the means to achieve neutral buoyancy, these fishes are easily able to hover or swim over the sediments. The snout-down inclination of halosaurs and macrourine rat-tails is seen to be related to the hydrodynamics of their (convergent) fin patterns.

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TABLE 2

FISHES REPORTED FROM DEPTHS GREATER  
THAN 150 METERS IN THE GULF OF ADEN

## BENTHIC FISHES

Scyliorhinidae	<i>Halaelurus indicus</i> (Brauer) <sup>1</sup>
	<i>Cephaloscyllium suflans</i> (Regan)
Triakidae	<i>Eridacnis radcliffei</i> Smith
Torpedinidae	<i>Heteronarce mollis</i> (Lloyd)
Rajidae	<i>Raja powelli</i> Alcock
	<i>R. johannis-davisi</i> Alcock
	<i>Raja</i> sp. egg capsule
Chimaeridae	<i>Harriotta</i> (?) <i>indica</i> (Garman) egg capsule
Alepocephalidae	<i>Alepocephalus bicolor</i> Alcock
Chlorophthalmidae	<i>Chlorophthalmus bicornis</i> Norman
Bathypteroidae	<i>Bathypterois atricolor</i> Alcock
Congridae	<i>Ariosoma guttulata</i> (Günther)
	<i>A. nigrimanus</i> Norman
Ophichthyidae	<i>Ophichthus multiserialis</i> Norman
Halosauridae	<i>Halosaurus parvipennis</i> Alcock
Macrouridae	<i>Macrurus firmisquamis</i> Gill & Towns <sup>1</sup>
	<i>Nezumia sclerorhynchus</i> (Valenciennes) <sup>1</sup>
	<i>Coryphaenoides wood-masoni</i> (Alcock) <sup>1</sup>
	<i>C. lophotes</i> (Alcock)?
	<i>Hymenocephalus heterolepis</i> (Alcock)
	<i>Bathygadus furvescens</i> Alcock
	<i>Gadomus multifilis</i> (Günther)
Moridae	<i>Physiculus roseus</i> Alcock
Trachichthyidae	<i>Hoplostethus</i> ( <i>Hoplostethus</i> ) <i>mediterraneus</i>
	Cuvier & Valenciennes
Bathyclupeidae	<i>Bathyclupea hoskynii</i> Alcock
Nemipteridae	<i>Parascolopsis townsendi</i> Boulenger
Bembropsidae	<i>Bembrops platyrhynchus</i> (Alcock)
	<i>B. adenensis</i> Norman
Uranoscopidae	<i>Uranoscopus crassiceps</i> Alcock
Gobiidae	<i>Gobius cometes</i> Alcock
Callionymidae	<i>Callionymus carebares</i> Alcock
Brotulidae	<i>Neobythites stacticus</i> Alcock
	<i>Dicrolene longimana</i> Smith & Radcliffe
	<i>D. nigricaudis</i> (Alcock)
	<i>Bassozetes glutinosus</i> (Alcock)
	<i>Porogadus trichiurus</i> (Alcock)
	<i>Glyptophidium macropus</i> Alcock
	<i>Luciobrotula bartschi</i> Smith & Radcliffe

<sup>1</sup> Records so marked are reported by Brauer (1906); the others are taken from Norman (1939). Where the authors are aware of changes, names conform to recent usage.

	<i>Catactyr squamiceps</i> (Lloyd)
	<i>Grammonus robustus</i> Smith & Radcliffe
	<i>Diplacanthopoma raniceps</i> Alcock
	<i>Mironus caudalis</i> Garman <sup>1</sup>
Scorpaenidae	<i>Phenacoscorpius adencensis</i> Norman
Triglidae	<i>Lepidotrigla omanensis</i> Regan
Synanciidae	<i>Minous inermis</i> Alcock
Bothidae	<i>Arnoglossus arabicus</i> Norman
	<i>Lacops nigriscens</i> Lloyd
Cynoglossidae	<i>Cynoglossus (Areliscus) acutirostris</i> Norman
	<i>Symphurus gilesii</i> (Alcock)
	<i>S. macrophthalmus</i> Norman
Lophiidae	<i>Chirolophius mutilis</i> (Alcock)
Ogeocephalidae	<i>Halicutoca fumosa</i> Alcock
	<i>Dibranchius nasutus</i> Alcock
	<i>D. obscurus</i> Brauer <sup>1</sup>
	<i>Coclophrys micropus</i> (Alcock)
BATHYPELAGIC FISHES	
Alepocephalidae	<i>Bathytroctes longifilis</i> Brauer <sup>1</sup>
	<i>Roulcina guentheri</i> (Alcock)
	<i>Xenodermichthys copei</i> Gill
	<i>Bajacalifornia burragei</i> Townsend & Nichols
Gonostomatidae	<i>Cyclothone signata</i> Garman var. <i>alba</i> , Brauer <sup>1</sup>
	<i>C. pallida</i> Brauer
	<i>C. acclinidens</i> Garman <sup>1</sup>
	<i>Yarrella corythaeola</i> (Alcock)
Sternoptychidae	<i>Argyrops ctenus affinis</i> Garman <sup>1</sup>
Chauliodontidae	<i>Chauliodus sloani</i> Bloch & Schneider <sup>1</sup>
	<i>C. pammelas</i> Alcock <sup>1</sup>
Stomiidae	<i>Stomias affinis</i> Gunther <sup>1</sup>
Malacosteidae	<i>Malacosteus niger</i> Ayres
Myctophidae	<i>Hygophum</i> sp. close to <i>reinhardti</i> (Lutken)
	<i>Diogenichthys laternatus</i> (Garman) <sup>1</sup>
	<i>Diaphus rafinesquei</i> (Coeco)
	<i>D. cocculeus</i> (Klunzinger)
	<i>Diaphus</i> sp.
	<i>Lampanyctus macropterus</i> (Brauer) <sup>1</sup>
	<i>L. nigrum</i> (Gunther) <sup>1</sup>
Nettastomidae	<i>Gavialiceps taeniola</i> Alcock
Nemichthyidae	<i>Aroettina infans</i> (Gunther) <sup>1</sup>
Melamphaidae	<i>Melamphaes megalops</i> Lutken <sup>1</sup>
Chilodipteridae	<i>Syngnops philippinensis</i> (Gunther)
Champsodontidae	<i>Champsodon omanensis</i> Regan
Trichiuridae	<i>Aphanopus carbo</i> Lowe
Oncirodidae	<i>Dolopichthys</i> sp.
Ceratiidae	<i>Cryptopsaras carunculatus</i> (Gunther)
	<i>Ceratias couesi</i> (Gill) <sup>1</sup>
	<i>Melanocetus</i> sp. ? <sup>1</sup>